dead plant and animal matter, this material is teeming with life. The basic processes of amonification, nitrogen fixation, and the synthesis of proteins are being carried on by these micro-organisms and the beetle which feeds upon this decaying matter profits by their activity. It has been shown, in the case of some insects, that under certain conditions the rate of growth is in direct proportion to the number of micro organisms in the food.

One has but to review the food lists of the beetles to note in how many cases they are known to feed upon fungi or upon substances which may well contain micro organisms. When this subject has been investigated further we may come to a newer and more rational undertsanding of the life cycle of the Coleoptera.

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7. THE LIFE CYCLE OF THE DIPTERA.

C. L. Metcalf, Ohio State University.

In attempting a summary such as this, one is almost dismayed by the great gaps in our knowledge of even the commonest species. Doubtless many of the gaps in what follows could be filled by a more careful scrutiny of the literature; many more, I am sure, could be filled from unpublished records and observations of the members of this Society; but when all this is recorded we shall find that very much more investigation must be performed before we can so much as give a comprehensive statement for all the species of a single family or for a single species of each family.

I do not believe that the order Diptera is surpassed, either within or without the class Insecta, for variety of habits and complexity of bionomics; and it seems to me an impossible task to present in a brief paper anything like a satisfactory picture of the life-cycle of the flies.

Not only is data wanting for more than a fraction of a per cent of the species; but, moreover, in the families where our knowledge is more complete, the most impressive thing is that *there is no agreement or uniformity of habit.* Where uniformity appears in my statements it is possibly because we know only a few of the many species in that group.

The Diptera all belong to the group variously known as Endopterygota or Holometabola or insects with a complete metamorphosis. Egg, larva, pupa and adult are very distinct from each other and usually well separated both structurally and ecologically. In fact, I have not been able to think of a single case in which the two active stages, larvæ and adults, occupy the same habitat and utilize the same kind of food. The nearest approach to it appears to be in some scavenger forms in which the adults and larvæ may both partake of the decaying material—in somewhat different condition, however; and the habitats of the two stages are very different. The blood-sucking habit is common for the adults, but the larvæ of these species have different habits. Even in the case of the obligate, parasitic, blood-sucking Hippoboscidæ, the larvæ are nourished, not by the host directly, but within the parent fly. And in the few cases where the larvæ are blood-sucking (Auchmeromyia) the adults appear not to do so.

If one were to point to a single factor which has had most influence upon the life cycle of the Diptera it would seem to be the habits of the larvæ. This, as we shall see, determines to a large extent the habitat of the egg and it has likewise a profound effect upon the specializations and adaptations of the pupa stage and to a lesser degree upon the habits of the adult, particularly upon oviposition.

Certain prominent lines of specialization are familiar to all. There are the aquatic species with their host of specializations and adaptations in egg-laying, for the maintenance of the egg in this precarious environment, for the locomotion, defense and respiration of the larva; for the maintenance and preservation of the pupa and for the emergence of the adult.

There are the numerous parasitic species with the perfection of the instincts for locating prey, many unique contrivances for safeguarding the eggs, interesting adaptations which enable the larva to reach its feeding grounds and to maintain itself variously as an external, a subcutaneous, a gastric, an intestinal, a nasal, an auricular or a vaginal parasite.

There are scavengers of all degrees of specialization; there are fruit flies and leaf miners and gall-making species and borers in root and stem; each showing peculiarities not encountered in the other groups and each, indeed, far removed from what must have been the original structure and habit of the ancestral forms.

The species of aquatic, scavenger, or parasitic habits are free from the restrictions governing the development of those species dependent upon living plants, but the life-cycle of the gall-makers, leaf miners and fruit flies is often built around the annual cycle of the host plant and we find many nice adaptations for the utilization of the potentialities of the plant tissues by attacking them at the exactly right time in their development.

THE EGG.

The egg stage shows many adaptations to its environment and in anticipation of the welfare of the subsequent larva.

The adults lack a definite ovipositor of chitinous appendages yet the terminal abdominal segments may be adapted to insert the eggs into the softer tissues of plants, fruits, etc., as in the Trypetidæ. Much more frequently the eggs are simply dropped, deposited, or glued to the surface of the substratum, on or in which the young may find nourishment. They may be (*a*) laid singly, (*b*) arranged in indefinite, irregular blotches or masses, (*c*) ranked with some definiteness but not fastened to each other, or (*d*) most carefully arranged in a definite manner with respect to each other, and fastened with a cement-like secretion. The cyrtid female expels the eggs forcibly in great numbers while hovering up and down a tree trunk (King*); conopids attach them to their host while in flight; sarcophagids will drop their young through a screen to food material some distance below. The interesting manner in which the female *Culex* holds the first few eggs upright between her crossed hind legs until enough can be fastened together to make the raft float has been described by Howard, et al.† Miall‡ describes some beautiful adaptations by which the eggs of aquatic Diptera are moored at the surface of the water. *Chironomus* eggs are laid in gelatinous ropes that are held in place by peculiarly twisted threads. The raft of *Culex* eggs floats by its own convexity, the single eggs of *Aedes* and *Anopheles* have curiously moulded air floats to decrease their specific gravity. The female ephydrid may crawl under water to fasten her eggs to submerged objects.

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*King, J. L. Observations on the Life History of Pterodontia flavipes Gray, *In* Annals Ent. Soc. Amer., IX, 3. Sept., 1916, 315.

†Howard, Dyar and Knab, The Mosquitoes of North and Central America and the West Indies.

‡Miall, L. C. The Natural History of Aquatic Insects.

All the eggs may be matured and extruded at one period, after which the female usually dies rather promptly. Among Leptidæ and Simuliidæ several females may contribute to the same egg-mass and their dead bodies are found together. Or the eggs may mature in definite batches at successive intervals. Or they may mature gradually and continuously and be laid over a period of several days as matured.

It is puzzling to explain certain indirect methods by which the larvæ are obliged to reach their proper feeding grounds. The human bot fly, *Dermatobia cyaniventris* is said to lay eggs on the bodies of a mosquito which serves as the porter for transference to a warm-blooded host, the contact with which causes prompt hatching. The well-known cases of the common Oestridæ in which the eggs are laid on a part of the body of the host remote from that occupied by the larva would seem to be a highly inefficient habit. The eggs of certain Syrphidæ may be laid on plants in anticipation of the usual subsequent infestation by aphids on which the young depend.

The duration in the egg stage is extremely varied, ranging from as few as four hours in the case of certain Muscidæ to commonly two or three days, or as many weeks. There are cases in which the winter is passed in the egg stage; or, most remarkable, where an entire year and a second winter of dormancy may be followed by successful hatching, as in certain mosquitoes.

As a rule, a considerable number of eggs are developed, but this varies even in a single family like the Tipulidæ from 45 to 2,000. Other species which are reputed to lay large numbers of eggs are certain Simuliidæ, Cyrtidæ, Trypetidæ, Muscidæ, and Tabanidæ. From the data I have noted it would seem that the average number of eggs per female is between 100 and 200.

THE LARVA.

The larval stage of the Diptera shows extreme specialization, being further removed from the typical arthropod condition than any other order. In the majority of the families this stage is a somewhat degenerated one and in many of them extremely so. True thoracic legs are always wanting and only rarely are pro-leg-like structures present. A definite head with well developed mouth parts and sensory organs is wanting in all the higher families. The condition of the spiracles also shows great reduction, frequently only an anterior pair and a posterior pair or group remaining.

The moults seem commonly to be three in number. The exuviæ are not as a rule prominent and often are entirely inconspicuous.

Organs especially adapting the larva to its environment are frequently noted. Curious suckers and pads for clinging to the surface of rocks in swift streams are exhibited by the Simuliidæ, Blepharoceridæ, etc. Peculiar stellate hairs for increasing surface tension are shown by *Anopheles*. One of the most interesting structures is the well known "rat-tail" or telescopic, posterior, breathing tube of certain Syrphidæ and Ephydridæ, which enables its possessor to feed from one to several inches under the water, while breathing air from the surface.

The majority of dipterous larvæ are aerial in respiration; Blepharoceridæ and Simuliidæ have tracheal or blood gills; while certain Psychodidæ have both open spiracles and functional gills; and the culicid larvæ accomplish respiration in part by spiracles, by gills, through the integument and per rectum.

Dipterous larvæ inhabit well-nigh every accessible haunt on the globe and feed on organic matter in every possible form.

Many are aquatic—Culicidæ, Simuliidæ, Blepharoceridæ and in part the Tipulidæ, Dixidæ, Chironomidæ, Rhyphidæ, Leptidæ, Stratiomyidæ, Tabanidæ, Ephydridæ, Sciomyzidæ, etc. Some of them prefer the clearest and swiftest of streams, others frequent open still water, some stagnant pools and some the foulest of liquids. In fact, practically every condition of water is utilized by some species of the single family Culicidæ. Certain chironomids are said to exist at depths of 1,000 feet.

The food of these aquatic larvæ is very varied and there is a definite correlation between the nature of the food and the specialization of head and mouth parts. Some devour microorganisms, others small plants, as algæ, others small animals and some doubtless the decaying organic materials themselves. Many species live in the soil, especially in moist soil or mud. Their food is either other small animals (Tabanidæ), or the decaying organic matter which contaminates the mud (Syrphidæ), or the roots and tissues of plants (Tipulidæ).

A host of species are found in decaying vegetable or animal matter in every possible stage of disintegration (Psychodidæ, Muscidæ, Drosophilidæ, Bibionidæ, Mydaidæ, Asilidæ, Heteroneuridæ, etc.) We have all marveled at the adaptations which enable an ephidrid fly to live as a larva in pools of crude petroleum, a substance highly toxic to almost all insect life.*

Compared with the Coleoptera, Lepidoptera, Hemiptera, and Orthoptera, Dipterous larvæ are rarely phytophagous on living plants. There are comparatively few crop pests. Yet many are leaf-miners, a good many feed in fruits, seeds, etc., a number are borers in the cambium and other parts of the trunks and stems and some feed exposed on the surface. The Cecidomyidæ or Itonididæ are almost exclusively phytophagous and exhibit the most remarkable and intricate and inexplicable adaptations to the abnormal plant structures they occasion and to securing food.

The larvæ of many Tabanidæ, Syrphidæ and Asilidæ are predaceous on insects and other small animals. Certain leptid larvæ are said to construct conical pitfalls for ensnaring prey, after the manner of ant-lions.

Many species of the Bombyliidæ, Phoridæ, Pipunculidæ, Conopidæ, Cordyluridæ, Sarcophagidæ and Tachinidæ are parasitic on other insects. A few are parasitic on warm-blooded animals, the Hippoboscidæ as ectoparasites, the Oestridæ and in part the Muscidæ, Sarcophagidæ and Syrphidæ as endoparasites. Certain species of the Muscidæ are unique in having larvæ which are intermittent blood-suckers on mammals and birds.

THE PUPA.

One of the most noteworthy features of this order is the clever manner in which the last larval exuvium is utilized as a protection for the pupa stage. Cases aside from the Diptera may be cited where the larva retains its exuvia, more or less mixed with excrement, as a covering during the quiescent transformation period, but I know of none which approach the diptera in the perfection of this habit.

In the suborder Cyclorrhapha entirely and in many of the Orthorrhapha the last molt is not cast at all, but becomes

*See Crawford, D. L., The Petroleum Fly in California. *In* Pomona Col. Jour. Ent. IV, 2, May, 1912, pp. 687-697.

inflated and indurated around the pupal membrane to form a complete, waterproof and resistant box within which the pupa stage is secure. A pair of thoracic spiracles is projected through this puparium for the respiration of the pupa. Quite as unique is the adaptation by which, in several dozen families, an inflatable sac, the ptilinum, is projected through the frons to dislodge the cap from the puparium and permit egress of the fly. So far as it is possible to formulate rules, it is the rule for the pupa stage to be passed in or near the larval habitat. In the case of aquatic or semi-aquatic larvæ the pupa is found in drier situations nearby. It is adapted to float on the water in the Psychodidæ, Chironomidæ, Stratiomyidæ and Ephydridæ. It may even survive successfully on the bottom of pools (Chironomidæ), or under water in streams or lakes, as in certain Simuliidæ, Blepharoceridæ and Ephydridæ.

In the case of the parasitic species the pupa may remain in the host (Conopidæ) or leave the host and seek protection on the ground (Tachinidæ and Oestridæ). In the ectoparasitic Hippoboscidæ this stage may be glued to the hairs or feathers of the host or lie on the ground.

As to the duration in the pupa stage we note the same variation as for the other stages. As a rule this stage is a rather short one, exceptionally occupying only a few hours, and commonly from a few days to a few weeks. But it is very often utilized as a hibernating stage, and in remarkable cases a second winter may be passed in this condition (Trypetidæ). This tendency of part of the brood to be delayed over an entire additional year as exhibited by the eggs of certain mosquitoes and the puparia of some fruit flies is a most inexplicable adaptation for the preservation of the species.

The exact length of the pupa stage is seldom recorded because of the fact that a prepupal stage of most irregular length may occur after the puparium becomes indurated before the change from larva to pupa takes place.

In the matter of activity of the pupa certain families of the Diptera are remarkable. The mosquito pupa swims about actively and avoids enemies in a manner most remarkable for a stage traditionally quiescent.

THE ADULT.

The adult stage is usually short lived, but is quite variable in the different families, and may even vary greatly in the same species, depending on the success of mating, feeding, etc. It is believed that in some species (Culicidæ, Oestridæ, etc.) the adults normally live only a few days and many forms probably never feed. Others lead a very active and vigorous life for some weeks or months as Trypetidæ, Drosophilidæ, Anthomyidæ, Muscidæ, Tachinidæ, Hippoboscidæ, etc. Certain adults have been kept alive well over a year.

Their haunts are almost as varied as those of the larvæ. Two conditions are especially favored:

(a) The vicinity of water in which the immature live. Here are found many Tipulidæ, Dixidæ, Chironomidæ, Blepharoceridæ, Ephydridæ, Cordyluridæ.

(b) Sunlight, which is especially effective on the activities of Tabanidæ, Syrphidæ, Bombyliidæ, Conopidæ and others.

The location of their own food is of course a dominating factor. The most noteworthy point regarding the food of adults is the complete specialization away from the primitive habit of defoliating plants. A very great number of species secure their food from flowers. The Tipulidæ, Culicidæ, Stratiomyidæ, Tabanidæ, Bombyliidæ, Syrphidæ, Conopidæ, Anthomyidæ, Muscidæ and Tachinidæ, are generally flower-feeders on nectar, or pollen, or both. Many species can feed on liquid organic matter or dissolve solid substances and sponge them up.

Species of the families Blepharoceridæ, Leptidæ, Asilidæ, Therevidæ, etc., are predaceous on small insects. In two families, the Tabanidæ and Simuliidæ, almost without exception, the females suck the blood of warm-blooded animals. Six other families are known to contain blood-sucking species—the Culicidæ, Chironomidæ, Psychodidæ, Muscidæ, Leptidæ and Hippoboscidæ. In only one family, the Muscidæ, do we find blood-sucking males, the males of the other families generally feeding on pollen, nectar, etc. Some of the Muscidæ feed on blood drawn by other insects (not being capable of drawing blood themselves) by inserting their proboscides at the side of those of their piercing relatives. A curious habit is recorded among the Hippoboscidæ, of individuals puncturing flies of their own kind and sucking the blood which the latter are drawing from the warm-blooded host. It is said that chains of these flies three or four individuals long may be found, taking the blood successively from their more fortunately (or unfortunately!) situated associates. The Hippoboscidæ are unique among permanent ectoparasites in possessing wings.

Blood appears to be especially effective on the development of the eggs. For example in certain Muscidæ several feedings of blood are necessary for the development of each batch of eggs. It is said that *Aedes calopus*, after feeding the first time, lays eggs and then becomes nocturnal in habit.

The mouth-parts of the adults, like those of many of the larvæ, are extremely specialized away from the ancestral condition. Within the family, however, they are, superficially at least, rather homogeneous; the species adapted for feeding in the several ways are hardly as diverse in structure as one would expect. The mouth-parts of the blood-sucking Muscidæ are probably unique among piercing insects in having the labium specialized as the cutting apparatus and adapted to enter the wound. The proboscis is rarely extremely elongated, an Indian tabanid having a beak an inch and a half long and three times the body length; this is probably used in probing flowers.

The number of generations a year varies in the Diptera from one, as in Oestridæ, certain Tipulidæ, Syrphidæ, etc., to two or three, which would seem to be the most common condition, (Tabanidæ, Cecidomyidæ, Sepsidæ, Syrphidæ, Trypetidæ, Anthomyidæ, etc.), to 7 or 8 in certain Muscidæ, 8 or 10 in some Trypetidæ, Simuliidæ and Culicidæ, and as many as 20 in Drosophilidæ.

The number is determined (1) by a certain inherent *minimum* time for each stage in each species and (2) by environmental conditions of heat, moisture, food, etc.

It may be said that the dipterous life cycle is noteworthy for *its shortness in certain species*, rather than for any remarkable prolongation or slowness of development. The shortest complete generation is about 10 days for the house fly, fruit fly, etc. while a duration of more than one year is very unusual.

The method of passing the winter is an interesting problem, but unfortunately one on which we have little information.

Any one of the stages may be adapted for hibernation; perhaps more often the pupa, then larva, adult and egg in the order named.

There are many curious mating habits among the Diptera. A common habit is to pair while dancing in swarms. In several cases the males emerge a little earlier and then await the emergence of the females, as in Simuliidæ and Tipulidæ. Indeed, the tipulid male is said to assist the female from the puparium. Oestrid males await about the host animal for the approach of the females. Secondary sexual ornaments of dolichopodid males are displayed before the females; while certain Empididæ construct frothy balloons to attract the females. In the Syrphidæ I have noted mating while hovering, (both facing the same way, male uppermost), and while resting on leaves, facing in opposite directions. In the latter case it may continue uninterruptedly for two or three days (*Temnostoma* spp.)

In methods of reproduction we find a very great range. Parthenogenesis seems not to have been developed in this order. Ordinarily, fertilized eggs are laid in the usual way. The Sarcophagidæ are all larviparous or ovoviviparous. The eggs hatch *in utero* and the active larvæ are extruded, in this family often being attached to a grasshopper or other host while both insects are in flight. The number of offspring per female in this family appears to be very high.

In the *Glossina* and Hippoboscidæ we find a remarkable condition, analogous to the vivipary in mammals, in that the larvæ derive all the nourishment for their growth and development from special glands in the uterus of the female. This, of course, reduces greatly the potential number of offspring; there are only six or eight per generation in the sheep tick.

Another remarkable condition known as paedogenesis is described for Miastor of the Cecidomyidæ. It is said that eggs are produced in ovary-like organs of the larva. These hatch and the young larvæ remain in the abdominal cavity feeding on larval parent tissues until they finally escape. A series of such multiplications is followed by pupation and a normal sexual reproduction of adults. The pupa of a species of *Chironomus* also reproduced parthenogenetically, according to Grimm.